INSTITUUT VOOR PLANTENZIEKTENKUNDIG ONDERZOEK
WAGENINGEN, NEDERLAND
DIRECTEUR: Dr. J. G. TEN HOUTEN

MEDEDELING No 158

PLANT TERATOLOGY AND PLANT PATHOLOGY

(PLANTENTERATOLOGIE EN PLANTEZIEKTENKUNDE)

DOOR

L. BOS

INVESTIGATIO PESTIBUS OBSTAT

N S P
R A M
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OVERDRUK UIT:
TIJDSCHR. O. PLANTEZ., 63:222-231, 1957

COMMONWEALTH MYCOLOGICAL INSTITUTE
15 SEP 195

PLANT TERATOLOGY AND PLANT PATHOLOGY

T. Pl.ziekten 63 (1957) : 222–231

PLANT TERATOLOGY AND PLANT PATHOLOGY[1])

Met een samenvatting: Plantenteratologie en Planteziektenkunde

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INTRODUCTION

Phenomena of abnormal growth have been known for a long time and have been studied repeatedly (e.g. fig. 1). Interest, especially concerning their physiology and aetiology, has increased during the last few decades. This may be demonstrated by the fact that a three day symposium was devoted to "abnormal and pathological plant growth" at the Brookhaven National Laboratory (U.S.A.) in 1953. The number of scientists participating in this conference was 182[2]).

Abnormal growth generally is able to induce two kinds of deviations, viz. those of histological (histoid) nature and those on the organ level (organoid). Amorphous growths of tissue, such as tumors e.g. those induced by *Bacterium tumefaciens*, and wound tissue, are of histoid nature. They are all changes in which no organs can be observed. Organoid deviations, on the contrary, are changes of entire organs or groups of organs; developmental patterns are changed and the morphology of the plant is different.

In the abovementioned symposium primary attention was given to the histoid aberrations, presumably largely as a consequence of a certain resemblance of these changes to animal and human cancers. (The investigations reported were supported in part by grants-in-aid from the American Cancer Society.) However, the organoid deviations are at least of equal importance. Numerous viruses can induce morphological deviations in the plant. RISCHKOV (1935) directed attention to this for the first time in a lecture on "filterable viruses and morphogenesis" (Filtrierbarer Virus und Formbildung). The relation of viruses to the growth of plants later was the subject of a paper by KUNKEL (1943). In the above symposium KUNKEL (1954) briefly reported on "virus-induced abnormalities". The important group of witches' broom virus diseases is characterized by organoid deviations.

Teratology is the branch of science which has long been studying morphological deviations in general. In this publication the significance of this science and of the accessory deviations for phytopathology will be discussed further on the basis of own research and the study of literature.

TERATOLOGY

Deviations in the exterior of the plant have been called *monstrosities* since early times. In the middle ages they were considered as indications of approaching disaster. Much later superstition gave way to serious scientific interest. In this way a more or less independent branch of science originated: *teratology*,

[1]) Aangenomen voor publikatie: 10–9–1957.

[2]) For a review of the report of this symposium published in 1954 cf. T. Pl.ziekten 61 (1955): 143.

practiced by many botanists. In 1841 the book "Éléments de Tératologie végétale, ou Histoire abrégée des anomalies de l'organisation dans les végétaux" appeared, written by MOQUIN-TANDON; a German translation followed in 1842. In 1869 the well known manual "Vegetable Teratology" by MASTERS was published; in 1886 translated into German. The "Principles of Plant Teratology" by WORSDELL (1915–1916) more or less gives a revision of the manual of MASTERS. Besides these publications an extensive literature was printed. Fig. 1 is taken from a communication of CONWENTZ (1878) entitled "Ueber aufgelöste und durchwachsene Himbeerblüthen". In his "Pflanzen-Teratologie", PENZIG gives a summarizing survey of the described deviations arranged according to the species in which they occurred. The first edition of this manual was published in 1890–1894, and the second edition of three volumes in 1921–1922. "Les Anomalies végétales" by VUILLEMIN (1926) is the most recent book on this subject.

The meaning of the name teratology usually is described as "the science of *monstrosities*, *abnormalities* or also of *malformations*". Summarizing they are spoken of as *teratomata*.

What is meant by these names? We cannot find an accurate definition anywhere; so there is much confusion concerning the limitation of the field of teratology. Subjects studied in literature on teratology appear to belong to the group of organoid growth deviations, the morphological deviations.

The meanings of "abnormal" and "deviation" often are subjects for discussion. According to VELENOVSKÝ (1905–1913) an organ is abnormal "wenn es sich anders ausgebildet hat als es in der Regel bei derselben Art statt zu finden pflegt". So in teratology they are talking of an abnormality when the normal variance is surpassed. From this it appears that it is very difficult to limit the field of abnormalities; there is no distinct borderline between modifications and abnormalities. Therefore, according to BLOCH (1954) it is better to call "abnormal" those structures and forms which are *markedly* different from those in a healthy individual typical of its species or higher category.

VENEMA (1949) adds to the above definition of abnormalities given by VELENOVSKÝ, the condition that their cause may not be of external origin. This conception presumably is promoted by the fact that in medicine teratology mostly is defined as "the science of *innate* malformations". In animal and human objects, however, the organoid deviations only can be of innate origin, because the organs are all formed before birth. In plants, on the contrary, during growth and development continuous initiation and formation of organs takes place.

According to the literature it appears that abnormalities, when the external cause is known, are most generally considered to be phytopathological phenomena. The deviations induced and inhabited by mites, insects or fungi, are commonly named galls (cecidia). In these cases the organoid deviations usually are attended with histoid tumefactions.

So literature demonstrates two tendencies: (1) to place *all* organ deviations in teratology, and (2) to restrict teratology to those deviations induced by a cause which is not of external origin.

Presumably to do both conceptions justice, notwithstanding the abovementioned remark, VENEMA (1949) distinguished between *primary teratological phenomena*, in which the genetic make-up is abnormal (due to an internal cause); and *secondary teratological phenomena*, when the genetic make-up is

normal but the organism develops abnormally (due to an external cause). In this way he names both groups of deviations teratological, but suggests that the latter group belongs more to phytopathology.

How can this dualism in the literature on teratology be explained?

Starting from the literal meaning of the name teratology (teras = wonder), in my opinion this branch of science concerns marvelous, inconceivable phenomena, deviating from normal, with an unknown cause. When a wonder is mentioned, this not only means the phenomenon, but especially the manner of origin and the inconceivability of it. Trusting this literal explanation and its preponderant use in literature, teratology means: "the science of morphological deviations caused by an unknown (perhaps mostly internal) factor".

In the meantime, however, the causes of many morphological deviations are discovered and studied by progressing science. Considering the abovementioned definition, the number of teratomata would decrease continually. Something like this is taking place in mycology. Formerly only the asexual method of reproduction of many fungi was known. Gradually the sexual reproduction phase of many is being discovered. In this way the number of *Fungi imperfecti* continuously decreases. In the same way teratology gradually would lose importance.

The names teratology and teratomata nevertheless have found their way into science. Like many other names they lost their original meaning. As a concept they take on new significance, adapted to the results of scientific research. So teratology now can be defined as "the science of morphological deviations". In my opinion these deviations should not be restricted to their cause, because it has been found that very different causes can induce similar morphological deviations.

Originally the causes of teratomata usually were not known, so teratology was restricted to describing and studying the morphology of the deviations. Teratology was, and generally still is, considered to be a subdivision of morphology. Nevertheless the study of causes also belongs to teratology. Without putting it into practice himself MASTERS (1869) writes: "Vegetable teratology comprises the history of the irregularities of growth and development in plants, and of the causes producing them". In medical science also, teratology consists of studying the phenomena themselves, the causal factors, the manner of origin, and the development of the malformations.

When in the literature on teratology facts about causes of the phenomena are mentioned, these often are based exclusively upon supposition; for the most part they are not founded upon experimental research. According to our present knowledge, morphological deviations may be due to the following factors: genetic disorders, nutritional factors, climatic factors, mites and insects, fungi, viruses (e.g. witches' broom viruses cf. p. 226), and growth substance treatment.

In studying the causal aspects of morphological deviations especially, we consider the fields of genetics, physiology, entomology and phytopathology. In

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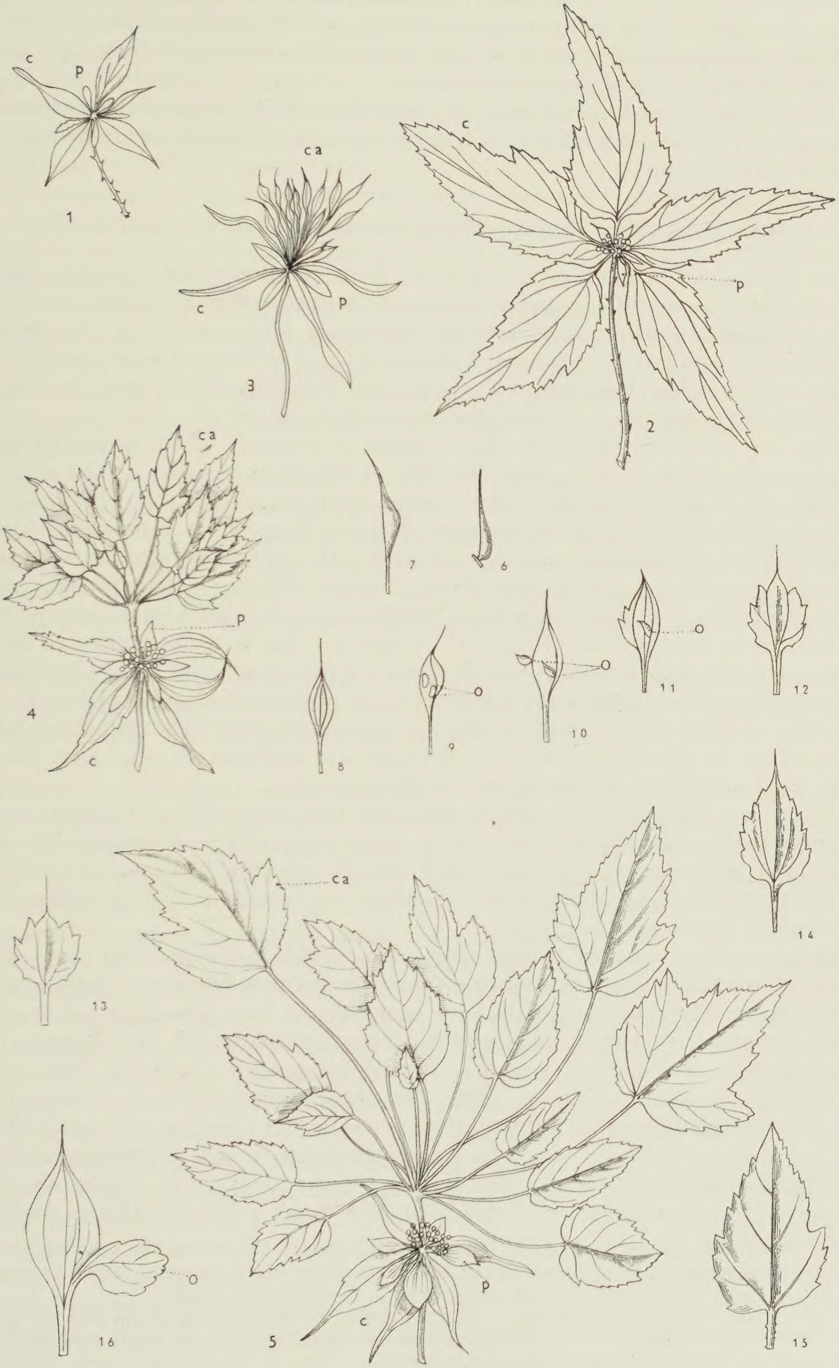
FIG. 1. *Rubus idaeus L.* Phenomena of antholysis, redrawn after CONWENTZ (1878): *1–5* abnormal flowers with phyllody, especially of the sepals (*c*) and the carpels (*ca*); *6–16* phyllody of the carpels; *p* petal, *o* ovule; (2/3 ×).

Rubus idaeus L. Bloemoplossingsverschijnselen, opnieuw getekend naar CONWENTZ (1878): 1–5 *abnormale bloemen met fyllodie, speciaal van de kelkbladen* (c) *en de vruchtbladen* (ca); 6–16 *fyllodie van de carpellen*; p *kroonblad*, o *zaadbeginsel*; (2/3 ×).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answering the question "how do all these factors act on morphogenesis", physiology and experimental morphology especially, must be taken into account. For a better understanding of the processes involved, knowledge of the morphology of the phenomena is of great importance.

Also in manuals of phytopathology, and those of the other abovementioned branches of science, a section or a chapter devoted to teratological phenomena surely will be in order.

THE SIGNIFICANCE OF TERATOLOGICAL PHENOMENA FOR PHYTOPATHOLOGY

In the second volume of this journal RITZEMA BOS (1904), introducing a communication on "Eenige misvormingen of monstrositeiten", briefly indicates the problem concerning the relation teratology–phytopathology. He agrees "that on the one side there is a good deal to be said in favour of a separation of these two branches of science, but on the other side (he) thinks it may be well to consider teratology as a subdivision of phytopathology".[1])

Starting from the definition that a plant is diseased when an incitant influences the plant in such a way that life of the plant or parts of the plant is threatened or influenced injuriously, many teratomata rightly can be included among phytopathological phenomena. The injurious effect is definitely more clear when the phenomena appear on a large scale (although here the adjective injurious also gets an anthropocentrical aspect). When, on the contrary, only one of the many flowers on a plant is abnormal, it is difficult to speak of a pathological phenomenon. From this it appears that it is not simple to draw a strict dividing line between abnormalities in a narrower sence and pathological phenomena. This is one of the reasons why in phytopathology attention has to be paid to teratomata. RITZEMA BOS has already pointed out "that those who give advise to practical persons on diseases and damages in cultivated plants also frequently have monstrosities" to diagnose.[2])

For a very long time the opinion prevailed that morphological deviations in plants would only appear incidentally. This supposition is presumably due largely to literature on teratology itself. Mostly one-sidedly attention was paid to the morphological aspect of the deviations and usually not to the degree and manner of appearance.

In my study of witches' broom virus diseases (1957) I found that these virus diseases are characterized by morphological deviations, being true pathological phenomena. These virus diseases have been known for a long time, occur on a large scale, and are very wide spread in all parts of the world. In Indonesia the witches' broom disease of peanuts (*Arachis hypogaea*), *Crotalaria*, and other crops has been known since 1908. The symptoms have been observed in 19 different plant species, belonging to five different families, and most likely all are due to the same virus. In the Netherlands, in the neighbourhood of Breda, the witches' broom virus disease ("dwergziekte") of raspberries has caused much damage since World War II. "Aster yellows", also a witches'

[1]) Hij schrijft: „Ik stem toe, dat er veel vóór is, de genoemde twee takken van wetenschap van elkaar te scheiden, maar vind toch aan den anderen kant, dat er ook veel vóór is te zeggen, de teratologie te beschouwen als een onderdeel van de phytopathologie".

[2]) RITZEMA BOS wees er reeds op, „dat aan degene, die zich onledig houdt met het geven van inlichtingen aan practici betreffende ziekten en beschadigingen van kultuurplanten, ook herhaaldelijk monstrositeiten worden toegezonden".

broom virus disease, occurring in the U.S.A., is able to affect about 300 different plant species belonging to 48 different families (KUNKEL, 1953). In Eastern and Central Europe "stolbur", a dreaded virus disease in Solanaceae, especially tomato, and other plant species, is occurring in increasing amounts. On account of the little attention paid by phytopathologists to the morphology of these symptoms, much confusion has developed, especially concerning the names. (For more facts refer to BOS, 1957).

So teratological phenomena not only have a morphological aspect but they have also phytopathological value. Therefore it may be clearer to replace the name teratology by *pathological-morphology* (patho-morphology) as GÄUMANN (1951) is doing already.

In contrast with morphological deviations in plant pathology, anatomical deviations are often studied (cf. the manual "Pathologische Pflanzenanatomie" by KÜSTER (1925)). For phytopathology the morphological deviations of the witches' broom virus diseases are at least as important as the often-cited anatomical deviations of such other virus diseases as necrosis of the phloem in potato leaf roll.

Nowadays morphology has an important physiological aspect (physiological- or experimental morphology). In this way patho-morphological research is able to play an important part in demonstrating how the pathogens in question interfere with the physiology of their host plants (cf. BOS, 1957). (For a discussion of the implications of recent work on the physiology of plant growth and development in relation to teratological phenomena cf. also HARRISON, 1952).

Accordingly it may be demonstrated how teratology or patho-morphology (and also morphology) is able to render an important service to plant pathology in aspects other than the purely diagnostic point of view.

Finally, the fact must be mentioned that literature on teratology contains valuable material for plant pathology. This may be demonstrated by fig. 1, pictured after CONWENTZ (1878). These deviations of raspberries closely resemble those which we now know are caused by the witches' broom virus of raspberries. On account of the limited facts furnished by the author, we cannot conclude that a witches' broom virus was the cause of the malady pictured.

In white clover, phenomena of virescence and phyllody are often observed. DE CANDOLLE described plants with abnormal inflorescences as a separate variety: *Trifolium repens* f. *viviparum*. This variety name refers to the fact that the virescent flowers readily develop roots in contact with the soil under humid conditions and in this way give new plants. Regarding the virescence PENZIG (1921) writes of white clover: "Vielleicht ist dies die Spezies in welcher derartige Verbildung am häufigsten verbreitet ist". BECKER (1941) is the first who supposes that at least a part of these phenomena in clover is due to a virus. A recent study (FRAZIER & POSNETTE, 1956) proved that greening and phyllody in clover indeed can be caused by a virus. The virus is transmissable by the leafhoppers (Cicadellidae) *Euscelis lineolatus* BRULLÉ and *Macrosteles viridigriseus* (EDWARDS). Lately EVENHUIS (1957) has demonstrated that in the Netherlands identical phenomena in red clover are due to a virus, also transmissable by leafhoppers to red clover, crimson clover (fig. 2), white clover, peas and china aster.

In this way presumably a large number of cases of antholysis, virescence and

FIG. 2. *Trifolium incarnatum L.* Virescence and phyllody, caused by a virus[1]): *1* normal flower; *2* raceme of a diseased plant; *3*, *4* abnormal flowers, enlargement of the sepals and phyllody of the carpel; *c* sepal, *p* petal, *ca* carpel (3 ×).
Trifolium incarnatum L. Vergroening en fyllodie veroorzaakt door een virus: 1 *normale bloem*; 2 *ziek bloemgestel*; 3, 4 *abnormale bloemen, vergroting van de kelkbladen en fyllodie van het vruchtblad*; c *kelkblad*, p *kroonblad*, ca *vruchtblad* (3 ×).

phyllody described in the extensive literature on teratology must be attributed to virus infections.

In this connection, from an historical point of view, the publications of PEYRITSCH (1882) on "Zur Aetiologie der Chloranthieën einiger *Arabis*-Arten" and that of HUGO DE VRIES (1896) on "Een epidemie van vergroeningen" are very important. They report the occurring, on a large scale, of phenomena of virescence. Their researches indicate the possibility of a virus transmitted by insects, causing the floral abnormalities.

PEYRITSCH succeeded in artificially inducing virescence in *Arabis*-species by means of an aphid (*Aphis* sp.). According to a casual remark by this author, the aphids, however, were taken from virescent *Arabis arcuata*-plants. Thus it is possible that the insects only acted as vectors of a virus.

DE VRIES observed in his experimental garden, also quite commonly, "virescences" in various plant species during the years 1893 and 1894. In 1893, 24 different plant species appeared to be affected. He studied the appearance and the spreading of the phenomena in detail and concluded that the deviations were not caused by gall mites. He reports: "Repeatedly I macroscopically and microscopically tried to find parasites, till yet without success, however. Especially *Crepis biennis*, *Agrostemma githago*, *Aster tripolium* and *Dipsacus syl-*

[1]) The material for this picture was kindly furnished by Drs. H. H. EVENHUIS, to whom I am greatly indebted.

vestris I often examined under the microscope in all sorts of stages of greening, without results, however" [1]). Moreover, gall mites usually are very specific, whereas here very different plant species showed symptoms. At the end of his research he had no more doubt as to the contagiousness of the phenomena. In 1894 the deviations occurred in a number of plant species. Some of which had also flowered in 1893, showing the same abnormalities. During that year the other ones still were in the rosette stage and in 1894 flowered for the first time, showing virescence. DE VRIES writes: "All these facts in my opinion point to a transport of the infectious matter by flying insects".[2]) His final conclusion reads: "that the presumable cause of the virescence overwinters in or on biennal or perennial plants, in these in the first place causing virescence, whereas from them it once more is able to infect other crops".[3])

Reading his publication we cannot help receiving the impression that DE VRIES most likely was studying a virus disease. Not being able to find a visible causative agent, he himself writes: "Therefore I have hesitated long before deciding to give out my observations. And now I am proceeding to do it, because the group of phenomena I observed during 1893 and 1894 so definitely gives the impression of an epidemic, that I no longer can doubt the contagiousness, although I did not find the parasite. *But I hope and trust that in this, other ones may be more successfull and I flatter myself with the thought, that the knowledge of the facts to be reported here, therefore will make the way somewhat easier*" [4]) (placed in italics by the present author).

In the french summary of his communication concerning the contagious agent DE VRIES writes about a "contagium". Two years afterwards BEIJERINCK (1898) started the famous name "contagium vivum fluidum" for the agent which later became known as the tobacco mosaic virus.

SUMMARY

Deviations from the normal morphology of the plant were long ago known by the names abnormalities, monstrosities or malformations. There are many kinds of abnormalities described in the extensive literature. Especially from a morphological point of view, they were originally studied by a more or less independent branch of science: teratology.

Teratomata are gradually being attributed to well defined causes. So this study, in an increasing rate, is removed to the field of plant pathology. With

[1]) „Herhaaldelijk heb ik getracht macroscopisch en microscopisch parasieten te vinden, doch dit is mij tot nu toe niet gelukt. Vooral vergroende *Crepis biennis*, *Agrostemma Githago*, *Aster Tripolium* en *Dipsacus sylvestris* heb ik meermalen en in allerlei stadiën der vergroening onder het microscoop onderzocht, doch zonder resultaat".

[2]) „Al deze feiten wijzen m.i. op een transport van de smetstof door vliegende insecten".

[3]) Zijn eindconclusie luidt „dat de vermoedelijke oorzaak der vergroeningen in of op tweejarige en overblijvende planten overwintert, deze zelven in de eerste plaats doet vergroenen, terwijl zij van hen uit wederom andere gewassen kan besmetten".

[4]) „Ik heb daarom lang geaarzeld, vóór ik besloot mijne waarnemingen aan anderen bekend te maken. En wanneer ik thans daartoe over ga, dan geschiedt dit, omdat de groep der verschijnselen die ik in 1893 en 1894 waarnam zoo geheel de indruk eener epidemie maken, dat ik aan de besmettelijkheid niet meer twijfelen kan, al heb ik den parasiet niet gevonden. *Maar ik hoop en vertrouw, dat anderen hierin gelukkiger zullen zijn, en vlei mij met de gedachte, dat wellicht de kennis van de hier te vermelden feiten den weg daartoe eenigszins gemakkelijker zal maken*" (cursivering van de schr.).

this, teratology as a science threatens to disappear gradually. Here, however, it is argued that plant teratology has to be: the science studying all aspects of deviations in the morphology of the plant. Because generally there is talk of disease symptoms, e.g. in the morphological deviations caused on a large scale by witches' broom viruses, perhaps it will be better to use the name pathological-morphology (or patho-morphology) in place of teratology. This name will give the impression that teratology is significant for plant pathology as well as for plant morphology.

The morphological study also appears to be able to give a better understanding of the way in which the various pathogens interfere in the physiology of their host and influence their morphogenetic action.

Giving some examples it is demonstrated how literature on teratology contains facts which, especially from an historical point of view, are valuable for plant pathology. From the research done by Hugo de Vries, on the occurrence and spread of epidemic phenomena of virescence during 1893 and 1894, it may be concluded that it was most likely a virus disease spread by insects.

SAMENVATTING

Afwijkingen in de uitwendige bouw van de plant zijn reeds zeer lang bekend als abnormaliteiten, monstruositeiten of misvormingen. In een omvangrijke literatuur zijn velerlei vormafwijkingen beschreven. Oorspronkelijk werden ze door een min of meer zelfstandige tak van wetenschap, de teratologie, hoofdzakelijk uit morfologisch gezichtspunt bestudeerd.

Het optreden van de teratologica blijkt steeds meer te herleiden te zijn tot duidelijk te omschrijven oorzaken, waardoor de studie in toenemende mate wordt verschoven naar het vakgebied der planteziektenkunde. Hiermee dreigt de teratologie als wetenschap geleidelijk te verdwijnen. Geargumenteerd wordt echter, dat onder plantenteratologie dient te worden verstaan: de tak van wetenschap, welke zich bezighoudt met alle aspecten van de afwijkingen der uitwendige bouw.

Omdat doorgaans sprake is van ziekteverschijnselen, zoals bij de vormafwijkingen welke op grote schaal veroorzaakt worden door heksenbezemvirussen, is het wellicht beter om in plaats van teratologie te spreken van pathologische morfologie. Deze naam brengt tot uitdrukking, dat de teratologie van betekenis is zowel voor de fytopathologie als voor de morfologie. Het morfologisch onderzoek blijkt tevens inzicht te kunnen geven in de wijze waarop de pathogenen de fysiologie der waardplant verstoren en hun morfogene werking uitoefenen.

Met enkele voorbeelden wordt aangetoond, hoe de teratologische literatuur voor de fytopathologie gegevens bevat, welke vooral uit historisch oogpunt waardevol zijn. Zo zijn de bloemoplossingsverschijnselen bij framboos, welke veroorzaakt worden door een heksenbezemvirus (dwergziekte), in de teratologische literatuur reeds lang bekend (fig. 1). Of ook deze door een virus werden veroorzaakt is niet met zekerheid na te gaan. Verschijnselen van vergroening en fyllodie bij klavers (fig. 2), waarvan onlangs is aangetoond dat ze door een virus kunnen worden veroorzaakt, zijn ook reeds lang bekend en zeer veelvuldig beschreven. Tenslotte kan uit het onderzoek dat Hugo de Vries instelde naar het optreden en de verspreiding van epidemische vergroeningsverschijnselen in

1893 en 1894, worden afgeleid dat het hier naar alle waarschijnlijkheid reeds ging om een virusziekte, welke door insekten werd verspreid.

ACKNOWLEDGEMENTS

The author wishes to express special thanks to Miss L. VAN DER BURG of the Department for Plant Taxonomy and Plant Geography of the Agricultural University, Wageningen, for making the drawings. He is greatly indebted to Prof. Dr. D. J. HAGEDORN, University Wisconsin, for help with the English text.

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